DIFFERENTIATION OF THE HUMAN CELLS OF SERTOLI.

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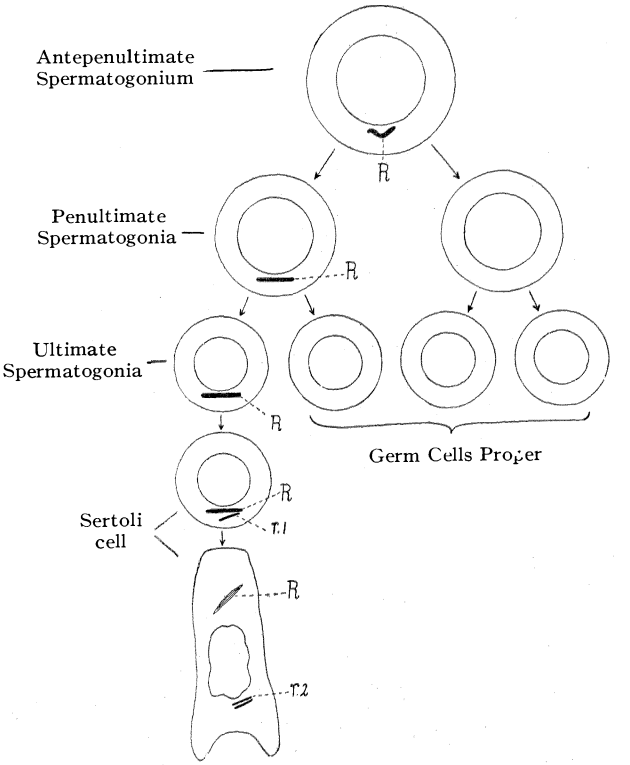
This study is based on the examination of the testis of a negro about 40 years of age, preserved in Zenker's fluid while still warm after his execution. The fixation was not as excellent as might be desired, cytoplasmic details being not always preserved, but the preservation of the nuclei was on the whole very good, and of spindle figures excellent. A considerable variety of staining methods were employed, of which the most fruitful proved to be Heidenhain's iron hæmatoxyline, with various degrees of extraction, followed by alcoholic eosin. Paraffine sections were made of 5μ and 8μ.

For the gift of this material I am indebted to the kindness of Dr. Addison, of the University of Pennsylvania.

1. GENERAL OUTLINE OF THE PROCESS.

The text diagram exhibits the chief results obtained. The antepenultimate spermatogonia contain each a rod (*R.*) within the cytoplasm. This does not divide in mitosis, consequently just half of their daughter cells, the penultimate spermatogonia, come to contain each a rod, while half of them lack it. In the division of these penultimate spermatogonia the rod does not divide but becomes distributed to one quarter of the ultimate spermatogonia. Each of every three ultimate spermatogonia produces by division two primary spermatocytes, and these cells which belong to the true germinal cycle lack the rod entirely. But each fourth ultimate spermatogonium preserves the rod, and this cell without further division enlarges and becomes a cell of Sertoli. In this cell of Sertoli a primary rodlet (*r. 1*) buds off from the rod; then the rod disappears, while the primary rodlet divides into two secondary rodlets (*r. 2*) and the latter persist in the Sertoli cell throughout its history.

The line of the Sertoli cell is therefore determined by the presence of the rod; one Sertoli cell is produced to every three



ultimate spermatogonia that lack the rod, or one Sertoli cell to every twenty-five spermatids.

2. The Antepenultimate Spermatogonia (Figs. 1–8, Pl. I.).

These are the largest germ cells in the adult testis, and like the other generations of spermatogonia are situated at the periphery of the seminiferous tubules. Frequently their nuclei are of irregular shape, as shown in Fig. 1. Within the nuclei (Fig. 3) are two kinds of nucleolar structures: acidophilic plasmosomes and basophilic bodies; it would take a detailed study to determine whether the latter are chromatoid nucleoli or modified chromosomes (allosomes). In their cell bodies are found chro-

matic rods, never more than one to a cell, various forms of which are drawn in Figs. 2–8, that of Fig. 5 being the largest found. The rods are homogeneous in appearance, dense, and they stain with basic stains but usually not as intensely as in the later spermatogonial generations. Such rods are usually in contact with the nuclear surface, but not always, and do not occupy constant positions with regard to the poles of the cell. Characteristic of the antepenultimate spermatogonia is the relatively small size of these rods and their frequently twisted form.

Thirty of these cells were carefully examined, and twenty-three of them showed each one rod. Of the remaining seven, five were not wholly within the plane of the section, so that their rods may have been present in the excised portions. It is probable that each cell of this generation comes to contain a rod, and that the rods are first produced in this generation; no spermatogonia of earlier generations were present, however, consequently there can be no surety of the latter point.

What the method of origin of these rods may be could not be determined. They are quite distinct from the idiozome, at least when fully formed, as shown in Fig. 2. In one case (Fig. 1) no rod was found but an irregular granular mass (x) which is possibly a precursor of the rod; if this be so, the rod might be considered to be produced by the conglomeration of granules at first scattered in the cell body. But the state of fixation of the cytoplasm was not sufficiently reliable to allow of any satisfactory determination of this matter. There is no evidence that the rods are directly produced from the nucleus. Their origin is thus unexplained, though their subsequent history is perfectly clear.

No mitoses of these cells were found, but there can be no doubt that the rods do not become divided for just half of the cells of the next generation contain rods.

3. The Penultimate Spermatogonia (Figs. 9–16).

Forty-nine cells of this generation were examined, care being taken to study only those that lay entirely within the plane of the section, and of these twenty-four exhibited each a rod while twenty-five showed no rods. Also six cases were found of two

nuclei in one cell body, indicating nuclear division without cytoplasmic division of antepenultimate spermatogonia: in all six of these cases only one rod was present, and an example is shown in Fig. 9. There can thus be no doubt that half the penultimate spermatogonia contain rods and half do not.

Characteristic appearances of the rods are illustrated in Figs. 9–11, Pl. I., 14–16, Pl. II. They differ on the average from those of the preceding generation in being usually larger, straighter, and more deeply-staining with hæmatoxyline, which indicates they have been undergoing growth changes.[1] Not infrequently they are curved around the nuclear surface (Fig. 14) and the length of a rod may equal the diameter of a nucleus. Consequently they are in this stage very prominent constituents of the cell bodies and easily differentiated by safranine or hæmatoxyline.

Mitoses of these cells were not frequent, but two clear cases (Pl. II., Figs. 12, 13) were found, showing that the rod (*R.*) passes undivided into one of the daughter cells, and this is fully borne out by a study of their distribution in cells of the following generation. Fig. 18 shows the end result of such a mitosis in a case where the cell body had not divided and here there is but one rod. What is the nature of the scattered globules shown in Figs. 12 and 13 is doubtful; they may be discharged nucleolar material.

4. The Ultimate Spermatogonia (Figs. 17–24, Pl. II.).

These are the smallest of the spermatogonia and the most numerous in the testis studied. One quarter of them contain each a rod; three quarters lack rods. One hundred and forty-two of these cells were studied, at stages before any of them had enlarged into Sertoli cells, the precaution being taken to include only cells lying wholly within the section; of these twenty-five showed each one rod, and one hundred and seventeen showed no rods. This ratio is somewhat less than 1 : 3, which is readily explained on the ground that some of the spermatogonia with rods had already become Sertoli cells and therefore were not included in the count. A very important and clear case is that

[1] The condition of the pair of rodlets (*r. 2*) in Fig. 10 will be explained later.

of Fig. 17; this shows four nuclei, the granddaughters of the nucleus of an antepenultimate spermatogonium, while there has been no division of the cell body, and it will be seen there is but one rod to the four nuclei. The evidence is then decisive that one quarter of the cells for this generation contain each one rod.[1] In these cells the rods are on the average more massive than in preceding generations (Figs. 17–24), and while usually more or less curved are never twisted. Quite frequently one end of the rod is bent off at an angle (Figs. 17, 22). In these cells also the rods are most dense and acquire their maximum stain, staining fully as intensely as the basichromatin; they generally but not always touch the nuclear surface.

5. Differentiation and History of the Sertoli Cells (Figs. 25–50).

All the ultimate spermatogonia that contain rods become cells of Sertoli, and those only. Nothing like either rods or rodlets were found in any of the spermatocytes or spermatids. The Sertoli cells become especially marked by their great growth. Fig. 25, Pl. II., shows the beginning of such growth, the Sertoli cell (*A*) growing out beyond its sister ultimate spermatogonia (*B* and *C*). Figs. 34 and 35, Pl. III., show Sertoli cells in a later growth stage in their entirety, and Figs. 36–39, 41–46 exhibit portions of them in still later stages. These cells became relatively enormous as shown in Fig. 50, Pl. V., which represents a portion of a transection of the wall of a seminiferous tubule; in this figure the shaded portion represents the bodies of the Sertoli cells, which have grown far into the lumen of the tubule to embrace the spermatids. This great growth is due mainly to the formation of vacuoles within the cytoplasm, and in the figures only the larger of the vacuoles are shown, not the great number of minute ones. These vacuoles are drops of a non-staining fluid, like that contained within the cavity of the tubule; only in rare instances are any concretions found in the vacuoles. One end, the basal, of each Sertoli cell remains adherent to the fibrous wall of the tubule and in the figures lines are drawn to denote

[1] Spermatogonia with two, three or four nuclei in a single cell body are unusually frequent and in such cases the sister nuclei are frequently of quite unequal volumes.

the inner border of the tubule; the other end, the distal, is the one that grows out and forms branches ramifying around the spermatocytes and spermatids. In the later history of the Sertoli cells large spaces are found within them, as shown in Fig. 50, which are cavities in which germ cells had been situated before their transformation into spermatozoa. Boundaries between the Sertoli cells become indistinguishable, so that these cells come to constitute a syncytial cytoplasmic net of extremely vacuolar structure (Fig. 50). In the basal portions of the Sertoli cells parallel bundles of fibrils may be seen at certain stages (Fig. 43).

The nuclear changes are also characteristic, and represent a gradual transformation of the structure of the resting nucleus of an ultimate spermatogonium. The reticulum changes first into microsomal masses (Fig. 25, Pl. II.). Then takes place a flowing of these masses together (Figs. 34–39, 41–43, Pl. III., IV.) until all the basichromatic substance of the nucleus becomes concentrated into a mass or karyosphere, and the particles remaining without the mass are oxychromatic. Figs. 44 and 45, Pl. V., represent the result of this process. Then follow stages of dissolution of the karyosphere into minute granules, all of which become gradually oxyphilic (Figs. 46 and 48), Fig. 49 representing a degenerate nucleus at the close of the cell's cycle. During all these stages the nuclei become very irregular, with deep indentations and lobations at their margins and grooves passing along their lengths. This irregularity of form and the central karyosphere are diagnostics by which these nuclei may be readily distinguished from those of neighboring germ cells. Further, the nuclei do not remain at the basal end of the cell, as they do in certain other mammals, but move out beyond the level of the spermatogonia (Fig. 50).

After passing through the series of changes just described the Sertoli cells degenerate, for there is no evidence that they go through a second cycle. This is proven by the later stages of these nuclei (Figs. 47–49) which gradually become wholly achromatic and then disappear from view. Their vacuolar substance must at that time mingle with the fluid of the tubule. Fig. 25 (Pl. II.) is interesting in this regard, for it exhibits a young Sertoli

cell (*A*) pushing out before it an old and degenerate one (*D*).

A Sertoli cell is therefore produced to every twenty-four spermatids, and after the latter have metamorphosed into spermatozoa and these spermatozoa have become discharged from the tubules, that Sertoli cell degenerates. Formation of Sertoli cells must then continue through life as long as formation of germ cells continues.

We now pass to the history of the rod in the Sertoli cells, that remarkable body which differentiates them from the functional germ cells. This is at first a simple rod, and may remain such even in the beginning enlargement of the cell (Fig. 25, Pl. II.). But this rod divides, and in most cases before the Sertoli cell begins its growth. Stages of its division are rarely found, and the only ones observed are illustrated in Figs. 26–30, Pl. III. It will be seen that in the cases of Figs. 26–28 the rod is undergoing an unequal longitudinal cleavage, a more slender and shorter rod abstricting from a portion of the larger one; this smaller rod may be called the primary rodlet. Perhaps one reason why these stages are so seldom found is because this division can be seen clearly only when the rod lies at a particular angle of vision. Whether Fig. 30 represents simply an unusually bent rod, or one that is in process of division, is hard to determine, for it was an isolated case. The condition immediately following this division is shown in Fig. 31, with an unusually long primary rodlet (*r. 1*) completely separated from the rod (*R.*); this is a cell body of the volume of that of an antepenultimate spermatogonium, where accordingly cytoplasmic division had not occurred, and where the original nucleus had divided while only one of its daughter nuclei had divided again. A case of rod and primary rodlet together at an unusually late stage is represented in Fig. 41, Pl. IV.

In four fifths of the cases, in 81 out of 100 cells examined, the large rod completely disappears before the Sertoli cell starts in its growth and in such cases only the primary rodlet is to be seen (Figs. 32–33, Pl. III.). Just so soon as the cell enlarges a pair of secondary rodlets are seen instead of the primary rodlet (Fig. 34), and without doubt these are produced by equal longitudinal cleavage of the primary rodlet, for they are always of

the same length and lie close together. In their later stages (Figs. 43, 46, 47) these secondary rodlets undergo some increase in thickening, and in all cases these rodlets persist within the Sertoli cell until the end of its cycle; they also probably degenerate there, for no signs of them were found within the germ cells or free in the fluid of the seminiferous tubule.

But in one fifth of the cases, 19 out of 100 cells examined, the original rod continues visible for a shorter or longer period after the secondary rodlets have been produced, as shown in Figs. 35–39, 42, 45; and in Fig. 41 is drawn an unusual case of late persistence of the rod and primary rodlet together. The rod may persist for a while as a single dense body (Fig. 38). Fig. 39 shows a case of such a single rod that has segregated into chromatic and achromatic parts, a rare condition. But as a rule it divides longitudinally as exhibited in Figs. 35–37, 41, 42, 45; this division begins and is most prominent near the middle region of the rod, when its ends may be still undivided, but cases were found where the rod had completely divided into two secondary rods (Figs. 35, 40, Fig. 40 being a rod from a cell of about the stage of the cell shown in Fig. 39). In the instances where the rod persists after the secondary rodlets have been produced, it never stains quite as deeply as the latter, and gradually becomes less and less chromatic until it can no longer be seen; no rod was observed in any cell after the karyosphere of the nucleus had disintegrated.

There is accordingly considerable individual variation in the behavior of the rod after it has abstricted the primary rodlet; in four fifths of the cells it then promptly disappears, in one fifth it persists for a variable period, but never until the end of the cycle of the Sertoli cell, and then undergoes a second longitudinal division which is this time an equal division. The rod when it persists generally remains in the basal portion of the cell body. The secondary rodlets are at first usually in contact with the surface of the nucleus, either basal or distal, while they are later found near the distal pole of the nucleus and usually separated from it. Whether the disappearing rod contributes substance to the formation of the fibers in the cytoplasm (Fig. 43) could not be determined. It is also difficult to decide whether the

rods and secondary rodlets are or are not always enclosed in vacuoles.

Certain aberrant cases need mention. In a single instance a pair of secondary rodlets were found together with a rod in a penultimate spermatogonium (Fig. 10), a precocious case of rodlet formation; what the constricted acidophilic body in the cytoplasm of this cell may be, I do not know. Then in each of two cases of rather late Sertoli cells, instead of the general case of one pair of secondary rodlets, two pairs were found (Figs. 44, 48); these might have been produced from an unusually long primary rodlet, such as the one shown in Fig. 31, by the occurrence of a transverse as well as a longitudinal division.

6. Discussion and Conclusion.

It is truly surprising that no thorough account has yet been given of the human cells of Sertoli; indeed, the studies made so far are rather histological than cytological.

Attention to these cells was first drawn by Sertoli (1865), who called them "cellule ramificati." Most writers since his time have given them his name; but the term "follicle cell" (coined by Valette St. George) is frequently employed, as well as the term "foot cell" (J. E. S. Moore), while v. Ebner ('71) employed the name spermatoblast, and Benda ('94) that of vegetative cell. The name follicle cell is generally used for the cells composing the spermatocysts of invertebrates and lower vertebrates, and that of Sertoli cell for the physiologically correspondent cells of mammaliam testes.

As to the genetic relations of the Sertoli cells to the germ cells proper the writers fall into groups, which Waldeyer ('06) has designated as the dualists and the monists. The first of these regard the two kinds of cells as of entirely different origin, the spermatogonia proceeding from primordial germ cells and the cells of Sertoli from other elements. As dualists are to be classed Watase, Bardeleben, Benda, Waldeyer and Stephan. Watase ('92) and Bardeleben ('97) consider the Sertoli cells to be interstitial testis cells that have wandered into the seminiferous tubules; but Bardeleben's figures are quite indecisive, and Watase, in his very brief account of little over a page, drew his conclusions from

the similarity in color of the cells of Sertoli and the interstitial cells after staining with cyanine, chromotrop and erythrosine. Though Bardeleben thus holds the two kinds of cells to be of different origin, he nevertheless thinks that the Sertoli cells give rise to "a rudimentary second form of spermatozomes." Benda ('94, '98), and Waldeyer relying upon him, considers the cell of Sertoli to arise from the indifferent cylindrical peritoneal cells. The dualists generally hold that a differentiated Sertoli cell remains functionally active during the life of the individual and does not regenerate more than the distal portion of its cell body; and they are also of the opinion that the cells of Sertoli proliferate themselves by division—amitotically, according to Bardeleben and Stephan, or mitotically according to Benda. On the other hand Prenant ('87), Schoenfeld ('01), Regaud ('99) and Bugnion ('06) consider both cells of Sertoli and spermatogonia to be derived from one kind of cells, by a process of division of labor; and this is in agreement with the results of most writers who have studied the origin of the follicular cells of the ovaries and testes of invertebrates—the follicular or nurse cell being generally regarded as a modified germ cell. Yet Regaud and Stephan ('02) hold that the fully formed Sertoli cells proliferate germ cells as well as nourish them; while Bugnion believes "the primordial spermatogonium gives place to a plurinucleate plate (part of the parietal synctium) which contains in a common cytoplasm spermatic nuclei and sertolian nuclei," after which the germ cells delimit themselves from the syncytium that remains as a Sertoli cell.

My conclusions differ practically in their entirety from those of the writers mentioned. In the human testis the cells of Sertoli are of common origin with the germ cells, one out of every four ultimate spermatogonia becoming a Sertoli cell. Sertoli cells are thus not differentiated from the germ cells merely in early fœtal history, but so long as ultimate spermatogonia continue to be produced. A Sertoli cell of man once differentiated does not, so far as I have observed, divide again, and consequently does not give rise to germ cells; further, a Sertoli cell dies completely after the spermatozoa that are associated with it depart from its surface, and it does not persist to nourish a second generation of spermatozoa. There being one Sertoli cell to every three defini-

tive ultimate spermatogonia there is necessarily one to every twenty-four spermatozoa; accordingly, in man the number of spermatozoa, spermatic bundle, associated with one Sertoli cell cannot be "8 or 16" as Bugnion states.

But the point of the greatest interest with regard to the differentiation of the human Sertoli cell, is that it is determined by the inclusion of a peculiar cytoplasmic rod, this rod first arising in the antepenultimate spermatogonia. No such "Sertoli cell determinant" has been made known in any other object. In the case of the differentiation of the oögonia from the nurse cells in the ovary of the beetle *Dytiscus*, so well described by Giardina ('01), and corroborated by Debaisieux ('09), there is a remarkable mechanism of differentiation of the nurse cells; here the cells that are to become oöcytes receive a cast-off reticular part of the nucleus, while the cells which lack this extruded mass become nurse cells. It will be seen that this is an entirely-different process from that described by me for man, for in man the Sertoli cells are those that contain the differentiating body.

The development of the human Sertoli cell is clearly a very beautiful case of somatic differentiation. In fact, one may regard the multicellular organism as having two periods of somatic differentiation: the first when the tissue cells become differentiated from the germ cells, and the second, when in the early mass of germ cells, the primordial gonad, the Sertoli cells become differentiated from the germ cells proper. For the Sertoli cells may properly be classed as the soma of the testis.

Nothing like the rod that differentiates the human Sertoli cells from the other ultimate spermatogonia seems to be known in any other case of somatic differentiation. In the classical case of *Ascaris*, discovered by Boveri, prospective body cells cast off into the cytoplasm the ends of their chromosomes. In copepods and insects, according to Häcker and Silvestri respectively, a nucleolus or a mass of nucleolar substance thrown out from the germinal vesicle of the egg comes ultimately to lie in cells of the germinal cycle. The origin of the rod of the human Sertoli cells I could not determine, beyond that it is first apparent in the cytoplasm of the antepenultimate spermatogonia, and that it probably forms there during the rest stage of the cells. It comes to develop in all antepenultimate spermatogonia, therefore, before

the distinction of Sertoli cells and germ cells; it becomes transmitted without division to one quarter of the ultimate spermatogonia, and that quarter transforms into Sertoli cells. Under these conditions, on account of the precision of the process, this rod must be regarded as a Sertoli determinant, and as a cytoplasmic and not a nuclear determinant. Whether the rod, or its substance, emanated in the first place from the nucleus, can be determined only by some fortunate observer who has more and better fixed material than was in my hands. But there is no reason to regard it as mitochondrial, as a chondriosome, because granular mitochondria have been described in mammalian Sertoli cells by Benda and others; in my material no mitochondria were seen in the spermatocytes and spermatids, they were evidently dissolved by the action of the fluid of Zenker, and it is therefore probable they were dissolved also out of the spermatogonia.

The rod that comes to determine the Sertoli cells increases in size while in the cytoplasm, becoming most voluminous in the ultimate spermatogonia; outside of the nucleus, also, occurs its process of abstriction of the primary rodlet and the division of the latter into the secondary rodlets. It is therefore clearly an extranuclear determinant of the Sertoli cell; and this as yet unique process of somatic differentiation seems to be controlled by an extranuclear body.

It has not been my intention to decide upon the function of the Sertoli cells. They increase greatly in size to produce a syncytial mass loaded with intracellular droplets, probably of fatty nature; they envelope closely the rapidly growing spermatocytes and for this reason they are generally supposed, and probably correctly so, to nourish this generation of germ cells. The fluid within the seminiferous tubules contains, so far as I have observed, neither erythrocytes nor leucocytes, therefore is probably derived from the droplets of the Sertoli cells and not from the blood serum. The spermatids at the commencement of their histogenesis lose their first connection with the Sertoli cells, while the nearly mature spermatozoa exhibit their heads buried in the substance of the Sertoli cells; the latter is then a second orientation of the germ cells to the Sertoli cells, one that cannot subserve nutrition, for the developing spermatozoa do not increase in size, but which is rather, as Loisel ('07) has shown, the expression

of some chemico-tactile response. It may then be the Sertoli cells fulfill three functions: to nourish the spermatocytes, to furnish the fluid within the seminiferous tubules, and to attract the spermatozoa into oriented bundles.

It is certain that much more study is needed of the Sertoli cells, both from the standpoint of somatic differentiation as well as that of the physiology of the germ cells themselves.

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EXPLANATION OF PLATES I–V.

All figures have been drawn by the author with the camera lucida at the level of the base of the microscope, and reduced one third in size in reproduction. Fig. 50 was drawn with Zeiss obj. C, ocular 12, all the others with the apochromatic immersion objective 1.5 mm., ocular 12.

The following abbreviations have been employed:

Id., idiozome.
R., rod.
r. 1, primary rodlet.
r. 2, secondary rodlets.
S.C., Sertoli cells.
Sp.G., ultimate spermatogonia.

PLATE I.

FIGS. 1–3. Entire antepenultimate spermatogonia.
FIGS. 4–8. Rods of antepenultimate spermatogonia.
FIG. 9. A binucleate penultimate spermatogonium.
FIGS. 10, 11. Penultimate spermatogonia.

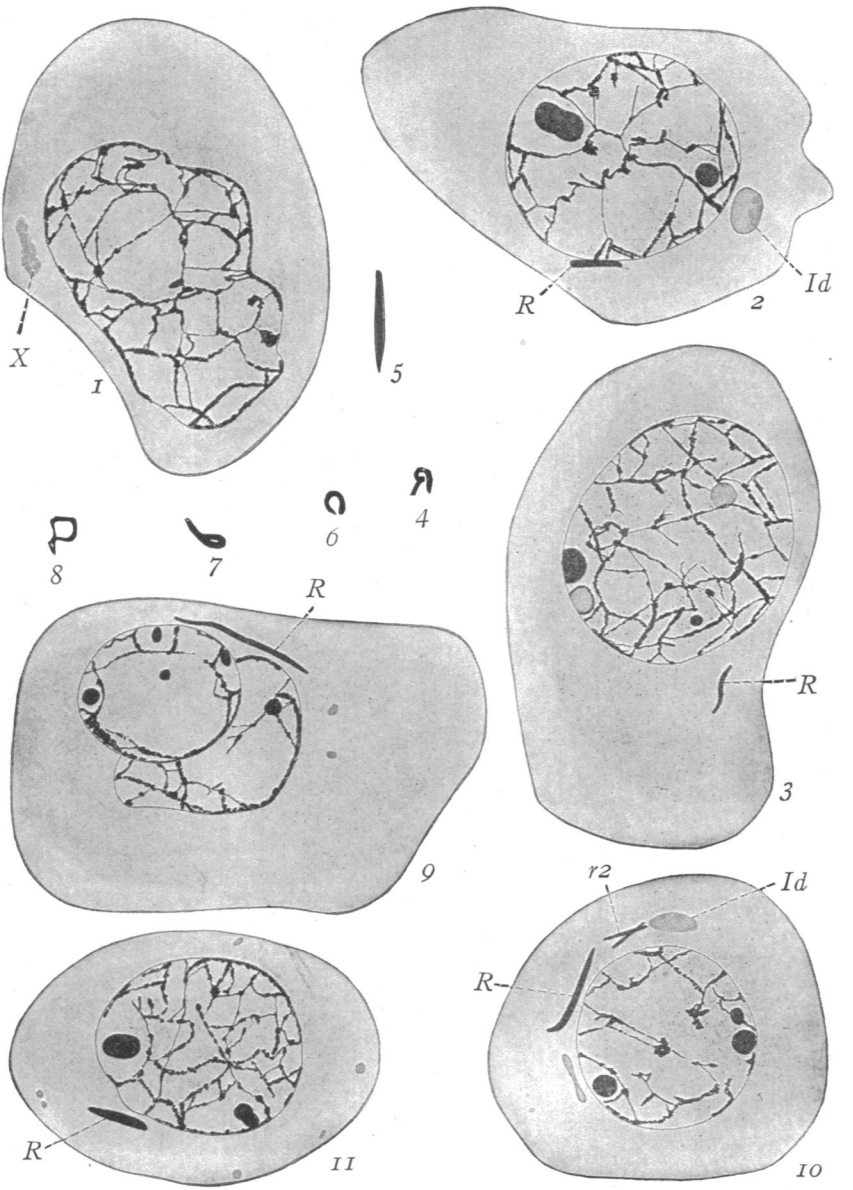

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PLATE II.

FIGS. 12, 13. Penultimate spermatogonia in division.

FIGS. 14–16. Rods of penultimate spermatogonia.

FIG. 17. Quadrinucleate ultimate spermatogonium.

FIG. 18. Binucleate ultimate spermatogonium.

FIGS. 19, 20. Ultimate spermatogonia.

FIGS. 21–24. Rods of ultimate spermatogonia.

FIG. 25. An incipient Sertoli cell (*A*) next to two ultimate spermatogonia (*B*, *C*), and to a degenerate Sertoli cell (*D*). The inner margin of the wall of the seminiferous tubule is at the left.

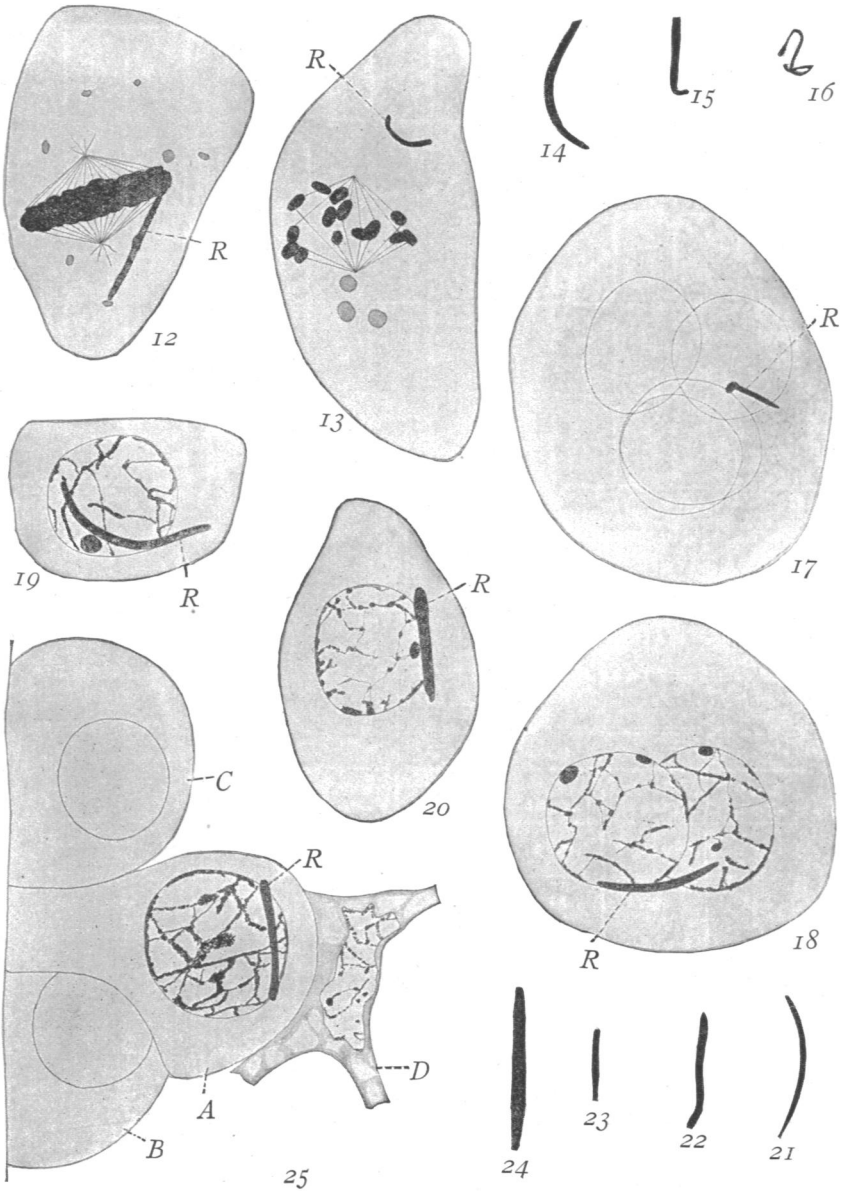

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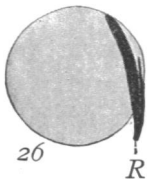
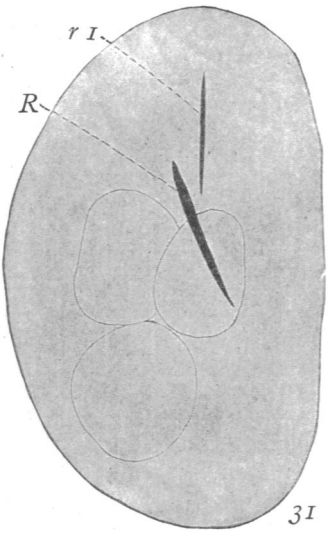
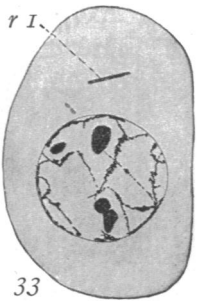
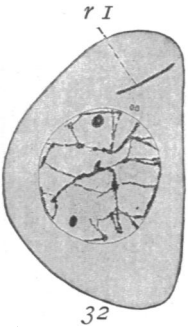
PLATE III.

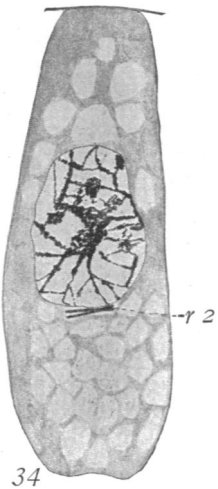
FIGS. 26–30. Primary rodlet abstricting from the rod, early Sertoli cells.
FIG. 31. Trinucleate ultimate spermatogonium.
FIGS 32, 33. Early Sertoli cells with primary rodlets.
FIGS. 34–36. Secondary stages of Sertoli cells.

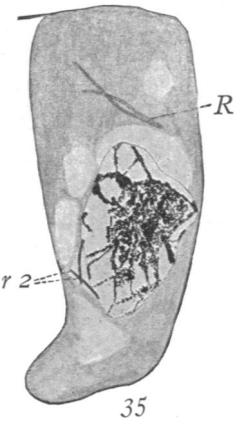












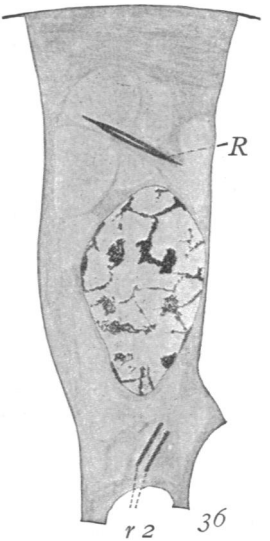


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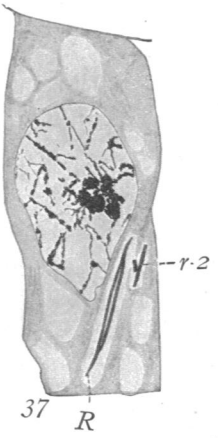
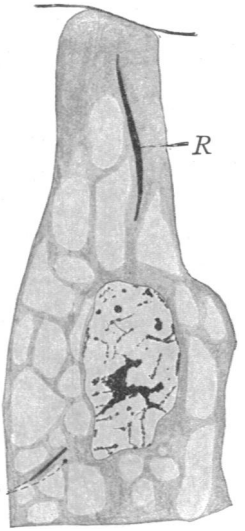
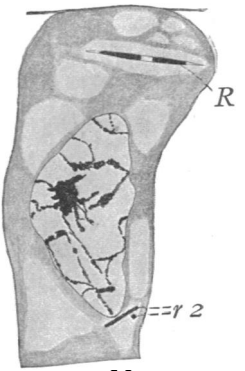
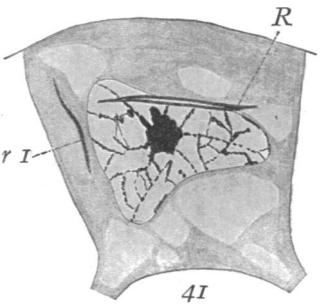
PLATE IV.

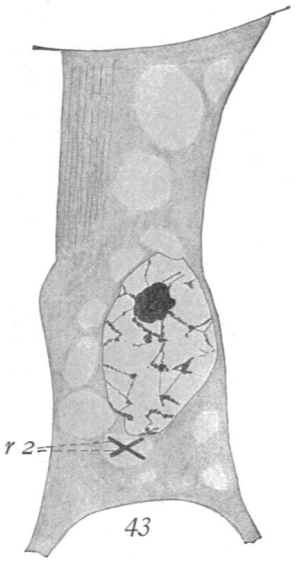
Succeeding stages of Sertoli cells arranged in the order of the nuclear changes Fig. 40 exhibits a dividing rod of a stage similar to that of 41.











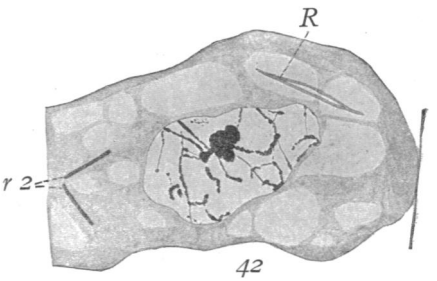


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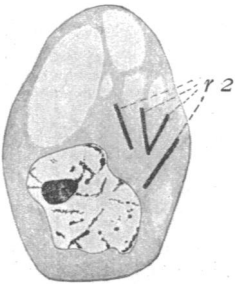
PLATE V.

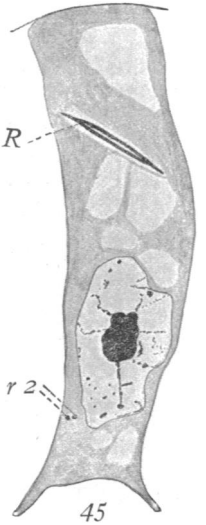
FIGS. 44–47. Later stages of Sertoli cells, Figs, 44 and 47 being oblique transsections.

FIGS. 48, 49. Degenerate nuclei of late Sertoli cells.

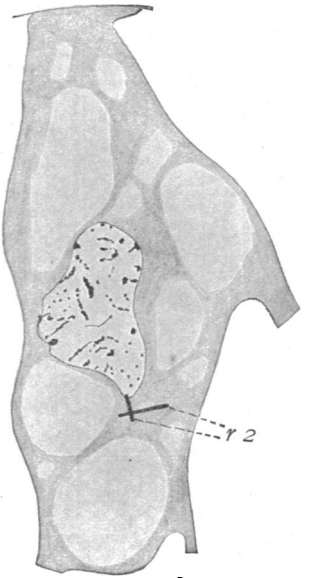
FIG. 50. Portion of a section of a seminiferous tubule. Uppermost is the wall of the tubule, and next to it a layer of ultimate spermatogonia. The syncytium of the Sertoli cells is expressed by dark shading, and their nuclei are distinguishable by their angular form and central chromatic body. The other cells shown are chiefly early spermatids.



44



45



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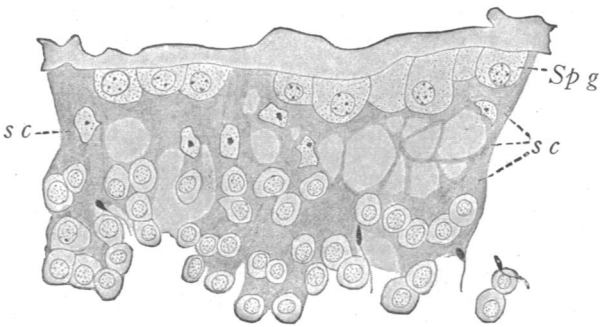

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